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Published in:
American Naturalist

Publication date:
1995

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American Naturalist, Volume 146, Issue 4 (Oct., 1995), 536-564.

Stable URL:
http://links.jstor.org/sici?sici=0003-0147%28199510%29146%3A4%3C536%3ACFNALI%3E2.0.CO%3B2-L

Vol. 146, No. 4 The American Naturalist October 1995

COMPETITION FOR NUTRIENTS AND LIGHT IN A MIXED WATER COLUMN: A THEORETICAL ANALYSIS

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Submitted March 31, 1994; Revised October 14, 1994; Accepted February 15, 1995

Abstract.—Interactions between nutrient limitation and light limitation are fundamental for the dynamics and structure of phytoplankton communities. We investigate a model that predicts the outcome of competition for nutrients and light in a mixed water column on the basis of monoculture characteristics. Growth in monoculture leads to a steady state. The nutrient availability and light penetration in this steady state characterize the minimal resource requirements of a species. These minimal requirements not only determine monoculture growth but also the outcome of competition. We show that competition for nutrients and light can be investigated by means of a graphical isocline approach. In contrast to earlier resource-based approaches, our model predicts that it is not only the ratio of nutrient supply to light supply that matters for the outcome of competition but also their absolute supply rates. It is even possible that a species that competes successfully when there is a high or low light supply is displaced when the light supply is intermediate. Factors such as mixing depth and background turbidity also affect the composition of phytoplankton communities. Still, our model predicts that at most two species can stably coexist in a mixed water column. Hence, the spatial heterogeneity imposed by a light gradient is not sufficient to solve Hutchinson's paradox of the plankton.

The observation that phytoplankton species compete for at most a handful of resources led Hutchinson (1961) to the formulation of his famous paradox of the plankton. Why do so many phytoplankton species coexist in an apparently homogeneous habitat? Many subsequent studies have suggested that temporal variability may explain the observed species diversity (see, e.g., Richerson et al. 1970; Levins 1979; Sommer 1985). An alternative solution to the paradox, however, is that even a well-mixed water column does not provide spatially homogeneous conditions for phytoplankton growth. Light, in particular, is never homogeneously distributed, since it forms a gradient over biomass and other light-absorbing substances. In fact, competition for light is mediated by shading and, thus, by the spatial heterogeneity created by the competitors themselves.

A simple model revealed that the heterogeneity of a light gradient is not sufficient to solve Hutchinson's paradox (Huisman and Weissing 1994). This model assumed that nutrients and light are perfectly essential resources (sensu Tilman

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Am. Nat. 1995. Vol. 146, pp. 536–564.

1980). That means we assumed that phytoplankton growth is either limited only by nutrients or limited only by light. There are, however, two reasons to expect interactions between nutrient and light limitation. First, nutrients such as nitrogen and phosphorus form an essential part of the photosynthetic machinery, whereas photosynthesis provides the energy required for nutrient acquisition. From a physiological perspective, we should thus expect interacting effects of nutrients and light on phototrophic growth (Rhee and Gotham 1981; Healey 1985; Riegman and Mur 1985). Second, the relative importance of nutrient and light limitation varies with depth. Algae will be relatively more nutrient limited when they face the high light intensities on top of a water column and become relatively more light limited when in the darker regions at the bottom. Could it be that the interactions between nutrient and light limitation allow many species to coexist in a light gradient?

In this article, we systematically analyze competition for nutrients and light in a mixed water column. We assume that nutrients and light are both (interactively) essential for phototrophic growth. However, we do not specify any particular relationship between nutrient and light limitation. Relying more on generality and less on specific equations makes the structure of our arguments more transparent and has the additional advantage that the conclusions will be quite robust.

We first investigate the growth of a monoculture. Knowledge of the resource requirements in monoculture is essential for the understanding of competition. We show that the dynamics of competition can be interpreted directly in terms of the minimal nutrient and light requirements of the competing species. This approach makes use of our previous results on light-limited growth and competition (Huisman and Weissing 1994; Weissing and Huisman 1994). It is an extension of earlier work on nutrient competition by, among others, Phillips (1973), Stewart and Levin (1973), Leon and Tumpson (1975), Taylor and Williams (1975), Tilman (1980, 1985), Hsu et al. (1981), Powell and Richerson (1985), and Butler and Wolkowicz (1987). Our model structure also shares several features with primary production models (see, e.g., Platt et al. 1988; Fasham et al. 1990; Slagstad and Støle-Hansen 1991), though these models usually aim at quantitative predictions of primary production while we are here more interested in a qualitative understanding of competitive interactions.

Throughout the analysis we emphasize the dependence of the outcome of competition on environmental conditions. Hence, our results may help to show how factors such as nutrient supply, mixing depth, and turbidity affect the species composition of phytoplankton communities.

GROWTH IN MONOCULTURE

In this section, we investigate the growth of a monoculture under nutrient- and light-limited conditions. We initially assume that light is absorbed only by biomass. Later, we consider the turbidity caused by other light absorbers such as water, detritus, or clay particles.

Model Structure

Biomass distribution.—We consider a well-mixed water column with a cross section of one unit area. Vertical positions within this column are indicated by the depth, s, where s runs from zero (top) to z (bottom). Let ω denote the biomass density. Because the water column is well mixed, we assume that biomass is uniformly distributed over depth. The cumulative amount of biomass above depth s, $w(s)$, is then simply given by the product of biomass density and depth; that is, $w(s) = \omega s$. In particular, the total biomass in the whole column, W, is given by $W = \omega z$.

Light absorption.—The water column is illuminated from above by a light supply with intensity I_{in}. According to Lambert-Beer's law, the light intensity I at depth s depends on I_{in} and on the cumulative amount of biomass above this depth:

$$I = I_{in} e^{-kw} = I_{in} e^{-k\omega s},$$

where k is the light extinction coefficient of biomass. Hence, the light intensity at the bottom of the water column, I_{out}, is a function of total biomass:

$$I_{out} = I_{in} e^{-kW}.$$

Specific production.—The rate of specific production (i.e., production per unit of biomass) depends on the availability of nutrients and light. Here we do not specify any particular equation describing this relationship. Instead, we only assume that the specific production rate, $p(I, R)$, is positively related to the light intensity, I, and the nutrient concentration, R:

$$\frac{\partial p}{\partial I} > 0 \quad \text{and} \quad \frac{\partial p}{\partial R} > 0. \tag{1}$$

Since nutrients and light are both essential for growth, we also assume that there is no production if light and/or nutrients are lacking:

$$p(0, R) = p(I, 0) = 0. \tag{2}$$

A simple example of a function $p(I, R)$ satisfying these assumptions is

$$p(I, R) = p_{max} \frac{I}{H + I} \frac{R}{M + R}.$$

This function, which combines two Monod terms in a multiplicative way, will be used in all our illustrations. It is clear, however, that assumptions (1) and (2) also apply to many other equations.

The specific growth rate, $g(I, R)$, is given by the difference between $p(I, R)$ and the specific loss rate, ℓ:

$$g(I, R) = p(I, R) - \ell.$$

The specific loss rate incorporates all sources of loss, including mortality, respiration, excretion, sedimentation, and so on.

Total production.—In order to quantify the total primary production in the water column, we have to evaluate the production at all depths. The "local production" at depth s is given by the product $p(I, R)\omega$ of specific production at depth s and the biomass density. The "total production," P, is then obtained by integrating the local production over depth:

$$P = \int_0^z p(I(w(s)), R)\,\omega\,ds\,.$$

The notation $p(I(w(s)),R)$ emphasizes the nested structure of our model, where p depends on I, I depends on w, and w depends on s. It is now easy to see that total primary production can also be quantified as an integral over cumulative biomass (Weissing and Huisman 1994):

$$P = \int_0^W p(I(w), R)\,dw\,.$$

We may thus interpret total production as a function of nutrient concentration and total biomass, as will be indicated by the notation $P(R, W)$. According to the fundamental theorem of calculus,

$$\frac{\partial P}{\partial W} = p(I(W), R) = p(I_{\text{out}}, R)\,. \tag{3}$$

That is, the increase of total primary production with increasing total biomass corresponds to the extra production obtained at the bottom of the light gradient.

Because the specific loss rate is assumed to be independent of depth, the total loss rate, L, is simply proportional to total biomass:

$$L = \int_0^z \ell\omega\,ds = \ell W\,.$$

Biomass dynamics.—The change in total biomass is given by the difference between total production and total losses:

$$\frac{dW}{dt} = \int_0^z g(I, R)\,\omega\,ds = P(R, W) - \ell W\,. \tag{4}$$

Nutrient dynamics.—Let the nutrient dynamics in the absence of primary producers be described by $dR/dt = S - DR$, where S is the nutrient supply rate and D is the rate coefficient of nutrient losses. Without consumption by primary producers the nutrient concentration settles at $R_{\text{in}} = S/D$. Nutrient consumption by primary producers is given by the product cP of tissue nutrient concentration, c, and total primary production. Note that total primary production is expressed in mass per unit of area while the nutrient concentration in the water column is given in mass per unit of volume. The total consumption cP must therefore be

divided by the mixing depth z in order to calculate the decrease in nutrient concentration. In summary, the nutrient dynamics becomes

$$\frac{dR}{dt} = D(R_{in} - R) - \frac{1}{z}cP(R, W). \tag{5}$$

Dynamics of Monoculture Growth

The dynamical system specified by equations (4) and (5) can be analyzed by standard phase-plane methods (see, e.g., Edelstein-Keshet 1988). In figure 1, we have depicted the biomass isocline (given by $dW/dt = 0$) and the nutrient isocline (given by $dR/dt = 0$) in the (R, W) plane. Some basic information on the shape of these isoclines is derived in appendix A. Let us here focus on the intuition behind the graphs.

The slope of the biomass isocline is positive because a higher nutrient availability can support more biomass. When nutrient availability is high, the isocline levels off because biomass remains bounded by the light supply. The biomass isocline must intersect the R-axis since growth can be sustained only if the nutrient availability exceeds a minimal threshold, R_C, defined by

$$p(I_{in}, R_C) = \ell \quad \text{or, equivalently,} \quad g(I_{in}, R_C) = 0.$$

The nutrient isocline has a negative slope. That means more biomass leads to more nutrient consumption and thereby to a reduced nutrient availability. The nutrient isocline does not intersect the W-axis because $dR/dt > 0$ for $R = 0$. In the absence of primary producers, the nutrient concentration settles at R_{in}. Thus, the nutrient isocline intersects the R-axis at the point $R = R_{in}$.

Hence, there are two scenarios. If $R_{in} < R_C$, the two isoclines do not intersect (fig. 1*A*). In this case, there is only one equilibrium state, in which $R = R_{in}$ and $W = 0$. The nutrient availability is simply too low to support any biomass.

If $R_{in} > R_C$, the two isoclines intersect in the interior equilibrium (R^*, W^*) (fig. 1*B*). There is only one interior equilibrium, because of the monotonicity of the isoclines. Whenever we discuss a variable evaluated at this equilibrium, it will be labeled with a superscript asterisk. The boundary equilibrium $(R_{in}, 0)$ still exists, but it is unstable since biomass will grow when close to zero. In fact, $g(I_{in}, R_{in}) > 0$ if $R_{in} > R_C$. In contrast, the interior equilibrium is locally stable (see app. C). Although local stability does not necessarily imply global stability, in all our simulations the system converged to this steady state. A typical trajectory is shown in figure 1*B*, where nutrients and biomass are introduced into an empty water column. Initially, the nutrient concentration rapidly increases. As soon as sufficient nutrients are available, the biomass starts growing. Nutrients are thereby consumed, and the nutrient concentration declines. This continues until the steady state (R^*, W^*) is reached.

A Resource-Based Approach

Primary production may be quantified not only in terms of depth or biomass, but also directly in terms of the light gradient. In fact, according to Lambert-Beer's law, light absorption per unit of depth is proportional to the local light

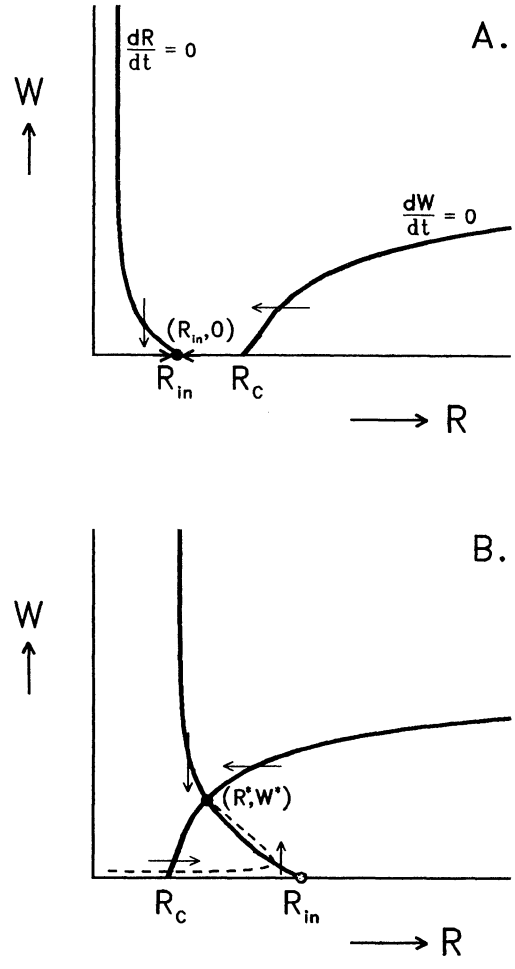

FIG. 1.—Plots of the nutrient isocline and the biomass isocline in the (R,W) plane. *A*, The case in which $R_{in} < R_C$. The nutrient input is too low to sustain biomass growth, and the system settles at the point $(R_{in}, 0)$. *B*, The case in which $R_{in} > R_C$. The nutrient input is sufficient to sustain growth, and the system settles at the interior equilibrium (R^*,W^*). *Dashed line*, a typical trajectory.

intensity; that is, $dI/ds = -k\omega I$. As a consequence, the biomass dynamics may be written as an integral over light intensity:

$$\frac{dW}{dt} = \int_0^z \frac{g(I,R)\omega}{-k\omega I}\frac{dI}{ds}\,ds = \int_{I_{out}}^{I_{in}} q(I,R)\,dI\,.$$

The integrand,

$$q(I,R) = \frac{g(I,R)}{kI}, \tag{6}$$

has been called the "quantum return" (Huisman and Weissing 1994; Weissing and Huisman 1994). The quantum return expresses the net growth per unit of light (i.e., per quantum) absorbed. In this sense, it resembles the physiological concept of quantum yield. Note that the quantum return depends on both light intensity and nutrient availability (in line with empirical observations; see, e.g., Cleveland et al. 1989). Hence, the total quantum return over the whole column may be viewed as a function of the nutrient concentration and the total amount of light absorbed, as summarized by the light intensity, I_{out}, at the bottom of the light gradient. For notational convenience, we introduce a function Q, which makes this dependence explicit:

$$Q(I_{out}, R) = \int_{I_{out}}^{I_{in}} q(I, R)\, dI . \tag{7}$$

The formulation of phytoplankton growth directly in terms of nutrient and light availability provides a better intuitive understanding of the biomass dynamics. For a given R, we may define a "compensation point" I_C such that the quantum return is positive above the compensation point and negative below the compensation point. Accordingly, the biomass dynamics can be split into two terms:

$$\frac{dW}{dt} = \int_{I_C}^{I_{in}} q(I, R)\, dI + \int_{I_{out}}^{I_C} q(I, R)\, dI .$$

The first term is positive and corresponds to the upper part of the light gradient, where production exceeds losses. The second term corresponds to the lower part of the light gradient and becomes negative as soon as the light intensity, I_{out}, at the bottom of the light gradient is reduced below the compensation point I_C. A steady state is reached when the positive quantum returns above the compensation point exactly balance the negative quantum returns below the compensation point. Thus, in the steady state, the quantum return at the bottom of the light gradient is negative. This implies that the specific growth rate at the bottom of the light gradient is also negative, that is,

$$g(I_{out}, R) < 0 \quad \text{for} \quad \frac{dW}{dt} = 0 . \tag{8}$$

In other words, the steady state of total biomass does not reflect a steady state at the local level. Instead, it is the balance between net gains at the top and net losses at the bottom that leads to a steady state of total biomass.

Using a geographical technique analogous to that of earlier resource-based approaches (see, e.g., Tilman 1982), we may plot a biomass isocline in the (R, I_{out}) plane (fig. 2). This isocline depicts all possible combinations of nutrient and light availability for which the total biomass remains stationary, that is, for which $Q(I_{out}, R) = 0$. Biomass will increase for all combinations of R and I_{out} above the isocline, and it will decrease for all combinations of R and I_{out} below the isocline. The slope of this isocline is negative (see app. A) because a higher nutrient availability leads to less light penetration. The isocline does not intersect the axes, since $dW/dt < 0$ for $I_{out} = 0$ or $R = 0$. In earlier resource-based approaches (e.g., Tilman 1982), the position of the biomass isocline did not depend on the

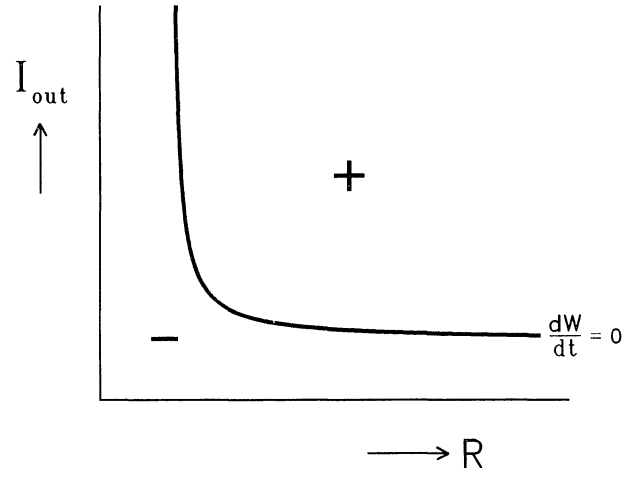

FIG. 2.—Plot of the biomass isocline in the (R, I_{out}) plane. Biomass increases for all combinations of R and I_{out} above the isocline, and it decreases for all combinations of R and I_{out} below the isocline.

resource supply rates. In contrast, according to equation (7) the position of the isocline in figure 2 depends on I_{in}. In fact, an increase of I_{in} shifts the biomass isocline toward the origin of the (R, I_{out}) plane (see Huisman and Weissing 1994). Thus, for each different light supply a new isocline has to be derived.

Background Turbidity

Thus far, we assumed that light is absorbed only by biomass. Let us now also consider the "background turbidity" caused by other light absorbers such as water, clay particles, and detritus. In this case, the light intensity at depth s is given by

$$I = I_{in} e^{-(k\omega + K_{bg})s},$$

where K_{bg} denotes the background turbidity. Now light intensity changes with depth according to $dI/ds = -(k\omega + K_{bg})I$. As a consequence, the biomass dynamics (eq. [4]) can be rewritten as

$$\frac{dW}{dt} = \int_0^z \frac{g(I, R)\omega}{-(k\omega + K_{bg})I} \frac{dI}{ds} ds = \frac{k\omega}{k\omega + K_{bg}} \int_{I_{in}}^{I_{out}} \frac{g(I, R)}{-kI} dI.$$

Hence, the biomass dynamics may again be interpreted in terms of the nutrient and light availability:

$$\frac{dW}{dt} = \frac{kW}{kW + K_{bg}z} Q(I_{out}, R). \tag{9}$$

In other words, for a given nutrient and light availability, the growth rate of biomass is reduced by the factor $kW/(kW + K_{bg}z)$ owing to the presence of other light absorbers (see also Bannister 1974). However, the position of the

biomass isocline in the (R, I_{out}) plane is not affected by other light absorbers. Biomass remains stationary if $Q(I_{out}, R) = 0$. Hence, the isocline depicted in figure 2 still characterizes the minimal resource requirements for phytoplankton growth.

MONOCULTURE CHARACTERISTICS ALONG ENVIRONMENTAL GRADIENTS

One may ask how the equilibrium biomass, light penetration, and nutrient concentration depend on environmental parameters such as nutrient supply, light supply, and mixing depth. In principle, this dependence can be investigated analytically (see app. B). Here we shall illustrate the relationships by the simulation results depicted in figure 3. In all simulations we varied one environmental parameter while the other parameters were kept constant.

Nutrient supply.—In line with intuitive expectation, our model predicts that a high nutrient supply supports more biomass than a low nutrient supply (fig. 3*A*). As a consequence, biomass absorbs almost all incident light in nutrient-rich habitats, while much light penetrates to the bottom of the water column in nutrient-poor habitats. Furthermore, the nutrient concentration increases when the nutrient supply is raised. Accordingly, nutrient and light availability are negatively correlated along a nutrient supply gradient (see also Tilman 1985).

Light supply.—A high incident light intensity is able to support more biomass than a low light supply (fig. 3*B*). More biomass consumes more nutrient, thereby depleting the nutrient concentration to a lower level. Interestingly, light penetration does not exhibit a monotonic trend. As long as light is limiting because of a low light supply, I^*_{out} is negatively related to I_{in} (see Huisman and Weissing 1994). When the light supply is increased, however, nutrients become limiting and biomass no longer keeps check on light penetration. Hence, I^*_{out} becomes positively related to I_{in}.

Background turbidity.—When the background turbidity is increased, more light is absorbed by other matter and hence less light remains for phytoplankton growth. Consequently, all else being equal, turbid waters (due to nonphytoplankton components) should support less phytoplankton biomass than waters with a low background turbidity (fig. 3*C*). In line with intuitive expectation, the model predicts that light penetration will decrease while nutrient concentration increases with increasing background turbidity.

Mixing depth.—Interestingly, biomass does not exhibit a monotonic trend along a gradient from shallow to deep mixing (fig. 3*D*). In a very shallow mixed layer, light is readily available but the total amount of nutrients (in g/m^2) is very low. As a consequence, nutrients are easily exhausted and total biomass remains low. An increase of the mixing depth first raises the total amount of biomass because more nutrients become available for growth. A further increase of the mixing depth, however, reduces total biomass because light becomes limiting when the phytoplankton is mixed to greater depths.

Loss rate.—In habitats where primary producers suffer considerable losses, biomass will be maintained at a low level compared with habitats with a low loss rate (fig. 3*E*). Fewer primary producers consume less nutrient and absorb less

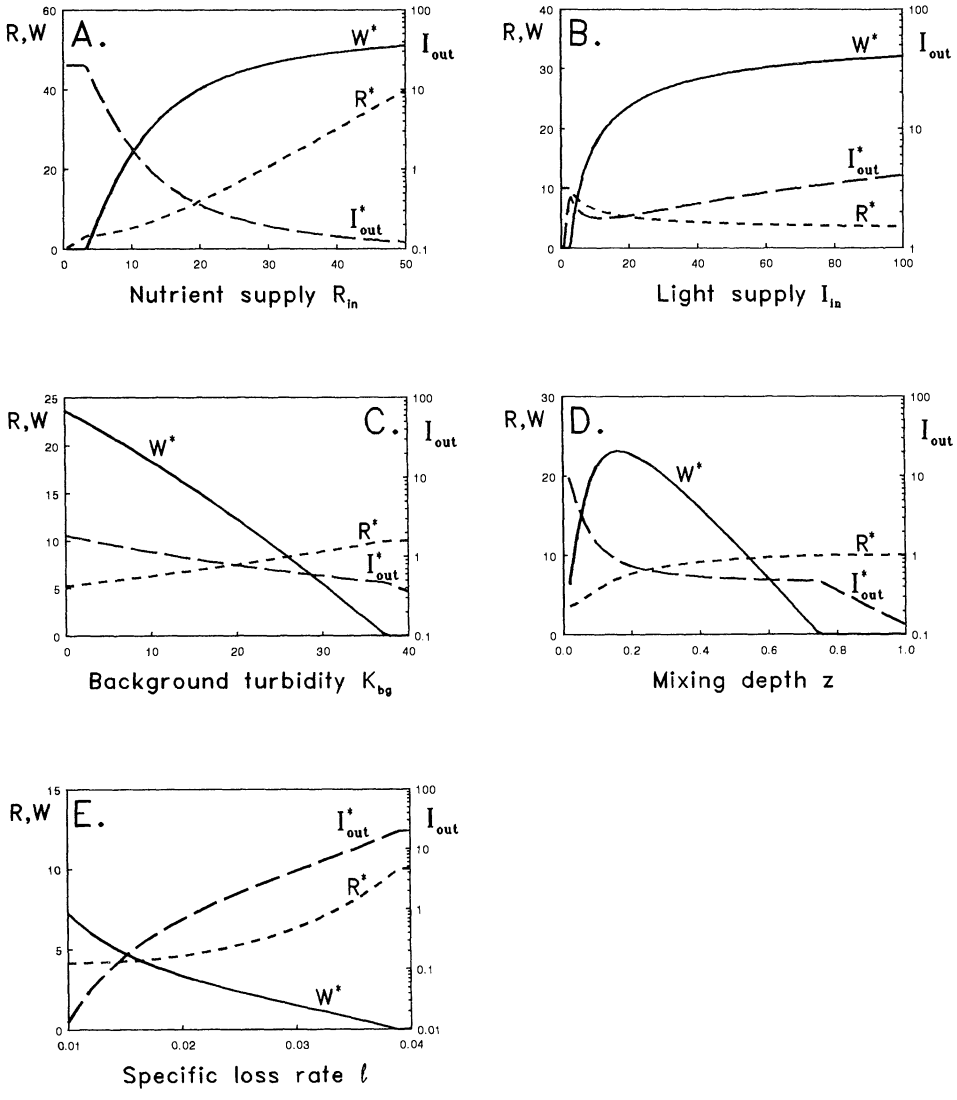

FIG. 3.—Equilibrium biomass (W^*), nutrient concentration (R^*), and light penetration (I_{out}) in relation to nutrient supply (*A*), light supply (*B*), background turbidity (*C*), mixing depth (*D*), and specific loss rate (*E*). In *E*, biomass should be multiplied by a factor of 10. Parameter values: maximum specific production rate (p_{max}) = 0.06; ℓ = 0.025; half saturation constant of light limitation (H) = 2; half saturation constant of nutrient limitation (M) = 4; c = 0.02; k = 0.1; D = 0.025; z = 0.1; I_{in} = 20; R_{in} = 10; in *A*, *B*, and *E*, K_{bg} = 0; in *D*, K_{bg} = 5.

light. Accordingly, both nutrient concentration and light penetration increase along a gradient from low to high loss rates.

COMPETITION FOR NUTRIENTS AND LIGHT

Let us now extend the analysis to a number of species growing together under nutrient- and light-limited conditions. The species are indicated by subscripts such as i and j. We assume that growth in mixture is governed by principles similar to those of growth in monoculture. Thus, the growth rate of a species i is given by

$$\frac{dW_i}{dt} = \int_0^z g_i(I, R)\omega_i ds = P_i - \ell_i W_i .$$

This formulation implies that growth is determined by the availability of nutrients and light. There is no direct interference between the species. The species interact only via nutrient consumption and light absorption. In fact, according to Lambert-Beer's law, the light intensity at depth s is

$$I = I_{\text{in}} e^{-(\Sigma k_j \omega_j + K_{\text{bg}})s} .$$

The nutrient dynamics is also a direct extension of the monoculture case:

$$\frac{dR}{dt} = D(R_{\text{in}} - R) - \frac{1}{z}\sum_{j=1}^{n} c_j P_j .$$

Partitioning of the Light Gradient

Analogous to earlier derivations (see eq. [9]), the dynamics of a species i in mixture may be written as

$$\frac{dW_i}{dt} = \frac{k_i W_i}{\Sigma k_j W_j + K_{\text{bg}} z} Q_i(I_{\text{out}}, R) . \tag{10}$$

This equation has a clear-cut interpretation. The first term, $k_i W_i/(\Sigma k_j W_j + K_{\text{bg}}z)$, describes the relative contribution of species i to the total light absorption. The second term, $Q_i(I_{\text{out}}, R)$, corresponds to the growth rate that species i would have attained under the same nutrient and light availability when grown in monoculture. In other words, equation (10) just states which fraction of the total light absorption is available for the growth of species i (see also Weissing and Huisman 1994).

Equation (10) shows that the growth rate in mixture has the same sign as the growth rate in monoculture. Accordingly, the isocline of species i, which was derived in monoculture (fig. 2), also specifies when species i is able to grow in mixture with other species: Species i will increase for all combinations (R, I_{out}) above its isocline, it will decrease for all (R, I_{out}) below its isocline, and it will remain stationary for all (R, I_{out}) on its isocline.

Competition Dynamics

When the isoclines of the competing species do not intersect, the species with the lowest isocline continues to grow until it has reduced the nutrient and light availability below the minimal requirements of all other species. Thus, in the end, only the species with the lowest isocline will survive.

In contrast, when the isoclines of two species intersect, as in figure 4, the point of intersection indicates an equilibrium state in which the two species may coexist. Since it is extremely unlikely and structurally unstable that more than two isoclines intersect in the same point, the possibility of equilibrium coexistence of more than two species can be neglected.

Consider two species whose isoclines intersect only once, in the point (R^*, I^*_{out}). Without loss of generality, we may label the species such that, at the point of intersection, the slope of the isocline of species 2 is steeper than the slope of the isocline of species 1 (as in fig. 4). Verbally, this means that, at the coexistence equilibrium, species 2 is relatively more nutrient limited than light limited when compared with species 1 (as in Leon and Tumpson 1975; Tilman 1980). It is important here to distinguish between local and global aspects of the water column. At a certain spatial position—for example, at the top of the light gradient—both species may be limited by nutrients rather than by light. The total growth rate of a species, however, is determined by integration of the local responses over the whole water column. In other words, only when "averaged" over the whole water column is species 2 relatively more nutrient limited while species 1 is relatively more light limited.

When nutrient supply is balanced by nutrient consumption (i.e., $dR/dt = 0$), the nutrient concentration is

$$R = R_{\text{in}} - \frac{1}{Dz}\sum_{j=1}^{2} c_j P_j . \tag{11}$$

Furthermore, according to Lambert-Beer's law, the light availability at the bottom of the light gradient, when measured on a logarithmic scale, is

$$\ln(I_{\text{out}}) = \ln(I_{\text{in}}) - K_{\text{bg}} z - \sum_{j=1}^{2} k_j W_j . \tag{12}$$

Equations (11) and (12) illustrate a fundamental difference between nutrient consumption and light absorption (Reynolds and Pacala 1993). While light absorption is related to the amount of biomass (W_j), nutrient consumption is related to the production (P_j) of new biomass. At equilibrium, production equals losses, and hence $P_j^* = \ell_j W_j^*$. Together with equations (11) and (12) this yields the biomasses at equilibrium:

$$W_1^* = \frac{k_2 z D(R_{\text{in}} - R^*) - c_2 \ell_2 (\ln(I_{\text{in}}) - K_{\text{bg}} z - \ln(I^*_{\text{out}}))}{c_1 \ell_1 k_2 - c_2 \ell_2 k_1}$$

and

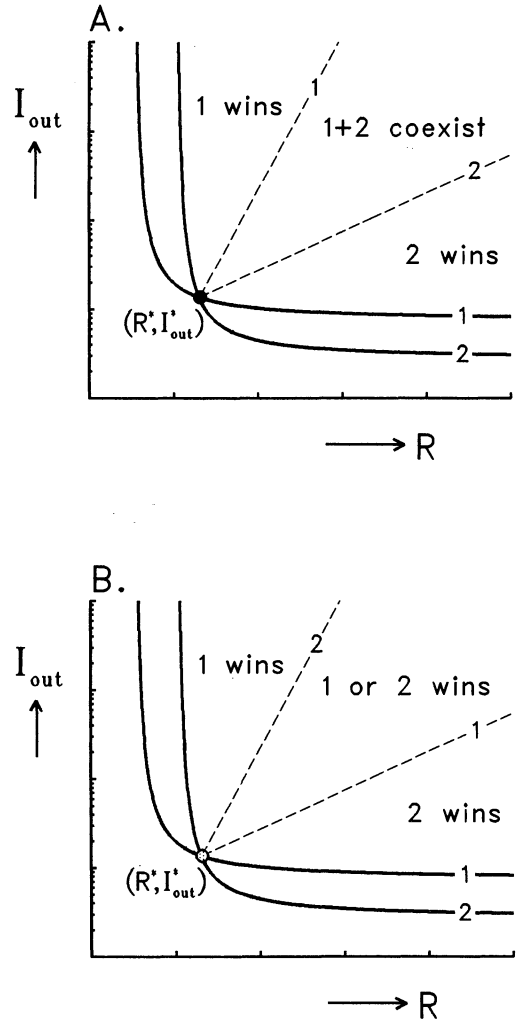

FIG. 4.—Graphical representation of two species competing for light and a nutrient in a mixed water column. The graphs show the isoclines (*solid lines*) and the consumption vectors (*dashed lines*) of species 1 and 2. In each region, the outcome of competition is indicated for supply points falling in that region. Note that the consumption vectors are straight lines, because I_{out} is expressed on a logarithmic scale. The isoclines intersect at the coexistence equilibrium (R^*, I^*_{out}). *A*, Stable coexistence equilibrium. The species stably coexist for all supply points falling in the region between the two consumption vectors. *B*, Reversal of consumption vectors and consequent unstable coexistence equilibrium. In this case, when the supply point falls in the middle region, either species 1 or species 2 wins the competition. The winner depends on the initial conditions.

$$W_2^* = \frac{-k_1 zD(R_{in} - R^*) + c_1\ell_1(\ln(I_{in}) - K_{bg}z - \ln(I_{out}^*))}{c_1\ell_1 k_2 - c_2\ell_2 k_1}.$$

Hence, equilibrium coexistence (i.e., both $W_1^* > 0$ and $W_2^* > 0$) requires either

$$\frac{k_1}{c_1\ell_1} > \frac{\ln(I_{in}) - K_{bg}z - \ln(I_{out}^*)}{zD(R_{in} - R^*)} > \frac{k_2}{c_2\ell_2} \tag{13a}$$

or

$$\frac{k_1}{c_1\ell_1} < \frac{\ln(I_{in}) - K_{bg}z - \ln(I_{out}^*)}{zD(R_{in} - R^*)} < \frac{k_2}{c_2\ell_2}. \tag{13b}$$

Appendix D shows that equilibrium coexistence is locally stable in the case of equation (13a), while it is locally unstable in the case of equation (13b).

These conditions can be interpreted graphically (see Tilman 1980). In figure 4 we have drawn two dashed lines in the (R, I_{out}) plane that intersect at the equilibrium point (R^*, I_{out}^*). These lines are analogous to the "consumption vectors" of Tilman (1980) and are given by

$$\ln(I_{out}) = \frac{k_1}{c_1\ell_1} zD(R - R^*) + \ln(I_{out}^*) \tag{14a}$$

and

$$\ln(I_{out}) = \frac{k_2}{c_2\ell_2} zD(R - R^*) + \ln(I_{out}^*) \tag{14b}$$

for species 1 and species 2, respectively. Note that the consumption vectors are straight lines in the (R, I_{out}) plane, because we scaled I_{out} logarithmically. In the same graph we may also plot a "supply point" (sensu Tilman 1980) with coordinates $R = R_{in}$ and $\ln(I_{out}) = \ln(I_{in}) - K_{bg}z$. According to equations (13), only those supply points that lie within the region bounded by the two consumption vectors allow equilibrium coexistence. However, whether equilibrium coexistence is stable depends on how the consumption vectors are arranged. Figure 4*A* corresponds to equation (13a); the consumption vector of species 1 is steeper than the consumption vector of species 2. In this case, the two species may stably coexist. Figure 4*B* corresponds to equation (13b). Here coexistence is unstable. Only one of the species will become dominant, but which species this will be depends on the initial conditions.

COMPETITION AND COMMUNITY STRUCTURE

The results outlined above resemble the approach pioneered by, among others, Leon and Tumpson (1975) and Tilman (1980). For example, our results are still consistent with the earlier finding that two species may stably coexist provided that each species consumes relatively more of the resource that limits its own growth more. However, there are also some important differences. In graphical terms, the positions of the isoclines depend not only on the growth and loss

characteristics of the species, but also on the light supply. The slopes of the consumption vectors (see eqq. [14]) depend not only on the consumption characteristics of the species, but also on their loss rates and on the mixing depth. The position of the supply point is determined not only by the nutrient and light supply, but also by the background turbidity and the mixing depth. Hence, the isoclines, the consumption vectors, and the supply point are not independent entities but are related to each other. For this reason, it is difficult to assess graphically how the species composition is affected by changes in, say, light supply, loss rate, or mixing depth. In order to illustrate how the outcome of competition is related to these environmental parameters, we have therefore resorted to computer simulations. In all our simulations, the parameter values were chosen such that unstable coexistence equilibria do not occur.

Figures 5 and 6 show the equilibrium outcome of competition for various combinations of nutrient and light supply. In figure 5, the species are ranked from species 4, having the highest maximal growth rate and the highest nutrient affinity, to species 1, with the lowest maximal growth rate and the lowest nutrient affinity. Species 4 is thus the superior nutrient competitor. However, species 4 is also a typical "sun species" that grows fast only at a high light intensity. Species 1 is more like a "shade species"; it performs much better at a low light intensity. Hence, as expected, species 4 displaces all other species when there is a high light supply. When the light supply is intermediate, species 4 still persists in habitats with a low nutrient availability, but species 2 and 3 take over in the nutrient-rich habitats where light becomes limiting (see fig. 3*A*). When the light supply is low, species 1 dominates in the nutrient-rich but rather dark habitats where light is the major limiting resource.

Figure 6 resembles figure 5 in that species 4 can still achieve the highest growth rate, while species 1 performs best at a low light intensity. However, in figure 6 there is also a trade-off between maximal growth rate and nutrient affinity. Species 1 has the lowest maximal growth rate but performs best at a low nutrient availability. Not surprisingly, then, the simulations predict that species 1 dominates both in low nutrient and in low light habitats, while species 4 is found only in habitats with a high nutrient availability and high light supply. The other species occur in between. It is obvious from figure 6 that it is not just the ratio of nutrient supply to light supply, but also the absolute supply rates that determine the outcome of competition. Hence, Tilman's (1982, 1985) resource-ratio hypothesis does not hold in the context of competition for nutrients and light.

Figure 7 illustrates the equilibrium community composition for various combinations of background turbidity and mixing depth. We used the same species characteristics as in figure 5. As shown previously (fig. 3*D*), nutrients are rapidly exhausted in a shallow mixed layer. Hence, species 4, which is the superior nutrient competitor, becomes the dominating species when the mixing depth is very low. With increasing mixing depth and/or background turbidity, nutrient concentration increases while light penetration decreases (see fig. 3). Hence, species 4 is gradually displaced by the other species when the mixed layer becomes deeper and/or more turbid. In the upper right corner of figure 7, light availability becomes too low to support any species at all.

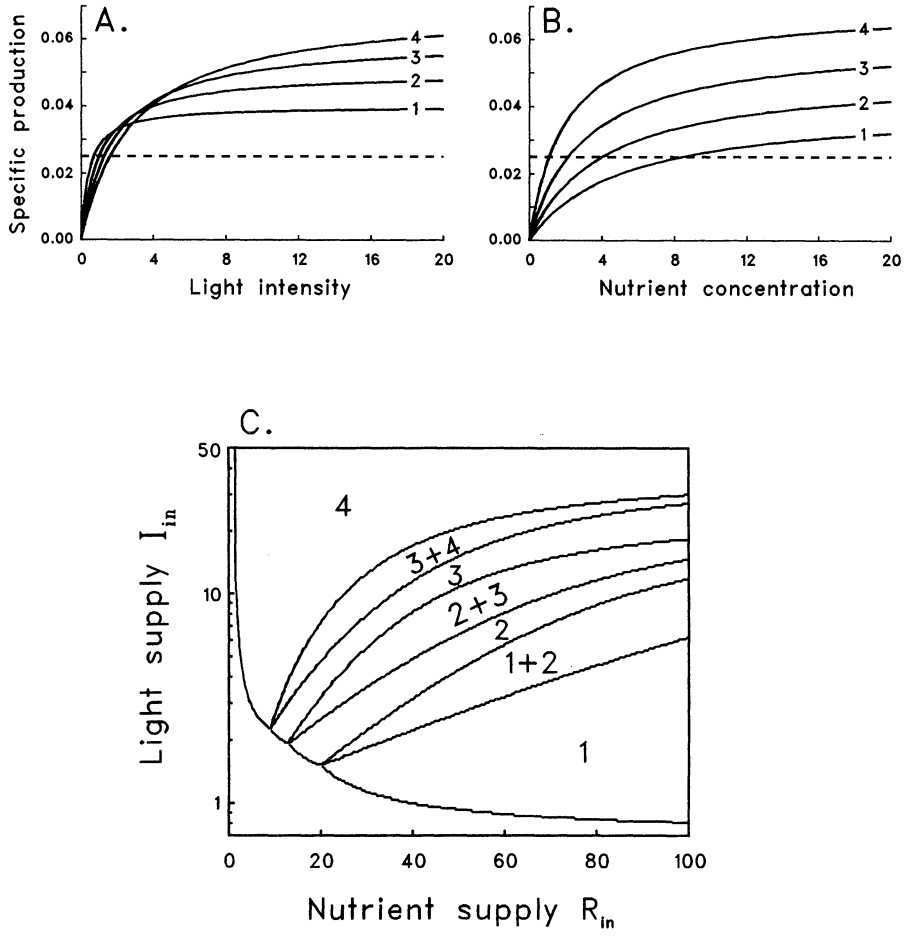

FIG. 5.—Competition of four species for nutrients and light in a mixed water column. The specific production rates of these species are shown in *A* and *B*. The dashed line indicates their specific loss rates. In *C*, the outcome of competition is shown for various combinations of the nutrient and light supply. Environmental parameters: $D = 0.01$; $z = 0.1$; $K_{bg} = 0$.

SPECIES PARAMETERS

Parameter	Species 1	Species 2	Species 3	Species 4
p_{max}	.04	.05	.06	.07
ℓ	.025	.025	.025	.025
H	.42	1	1.8	2.9
M	5	4	3	2
c	.05	.04	.03	.02
k	.05	.08	.12	.16

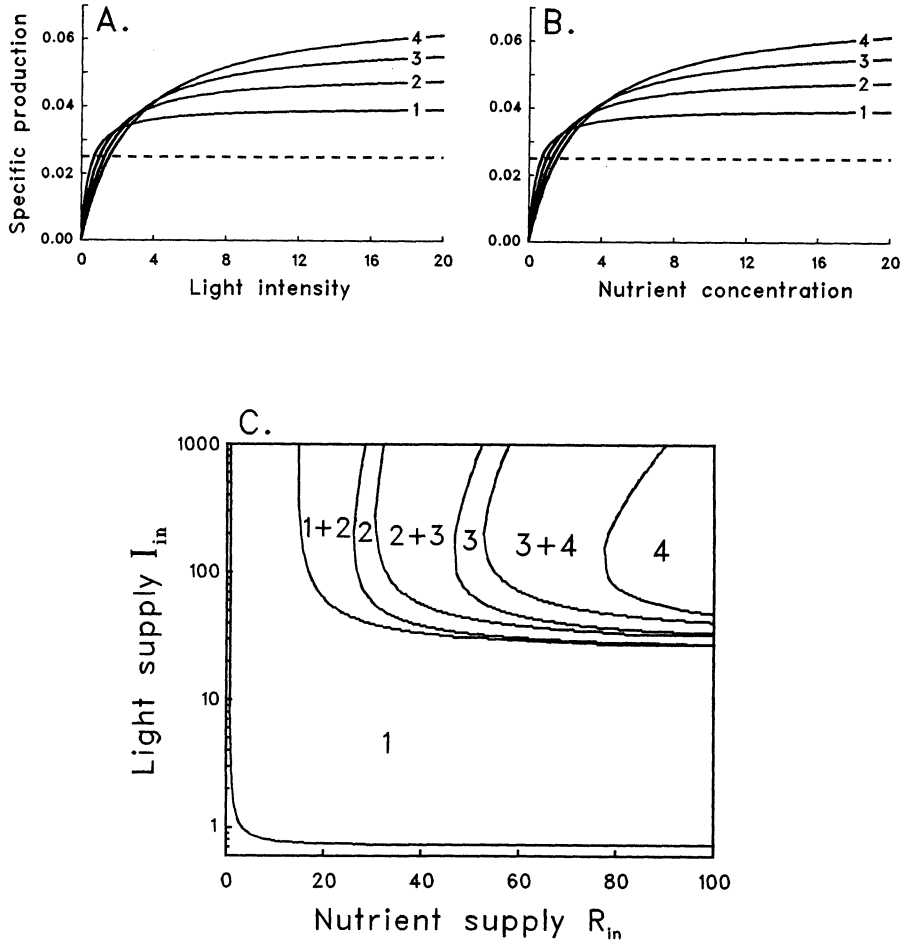

FIG. 6.—As in the previous figure, four species compete for nutrients and light. The specific production rates of the species are shown in *A* and *B*. The dashed line indicates their specific loss rates. In *C*, the outcome of competition is shown for various combinations of the nutrient and light supply. Environmental parameters: $D = 0.01$; $z = 0.1$; $K_{bg} = 0$.

SPECIES PARAMETERS

Parameter	Species 1	Species 2	Species 3	Species 4
p_{max}	.04	.05	.06	.07
ℓ	.025	.025	.025	.025
H	.42	1	1.8	2.8
M	.42	1	1.8	2.8
c	.01	.02	.03	.04
k	.28	.24	.20	.16

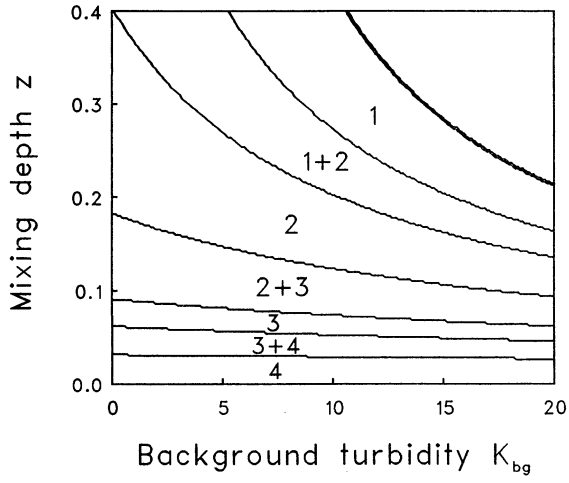

FIG. 7.—The outcome of competition under various combinations of background turbidity and mixing depth. The species are the same as in fig. 5. Environmental parameters: D = 0.01; I_{in} = 10; R_{in} = 50.

In figure 8, we varied the loss rate. Again we used the species characteristics depicted in figure 5. Species 1 dominates at the low light availability encountered at a low loss rate, while species 4 can withstand the high losses encountered at a high loss rate. Interestingly, species 3 exhibits a "bimodal" response. It occurs in combination with species 1 at a low specific loss rate, is displaced by species 2 at an intermediate loss rate, but reappears when the loss rate is further increased. Basically, what happens is that the isoclines depicted in figure 4 start "moving" when the losses are increased. However, the isoclines do not move at the same rate. When losses are low, the isocline of species 3 lies below the isocline of species 2. With an increase of the loss rate, the isocline of species 3 gets above the isocline of species 2. Hence, species 3 is displaced. A further increase of the loss rate, however, shifts the isocline of species 2 again above the isocline of species 3, and species 3 returns.

In Tilman's (1980) original approach, the isocline positions are independent of the resource supply. When species compete for nutrients and light, however, the isocline pattern varies with the light supply. As a consequence, a bimodal response to a change in the light supply is also easily conceivable. Consider, for example, figure 6. For a nutrient supply R_{in} = 80, species 3 coexists with species 4 both below a light supply I_{in} = 70 and above a light supply I_{in} = 300. However, species 3 is displaced by species 4 for all light supplies in between.

DISCUSSION

Minimal Resource Requirements for Phytoplankton Growth

Well-mixed aquatic environments do not provide homogeneous conditions for phytoplankton growth. Instead, algae have to cope with a gradient from high

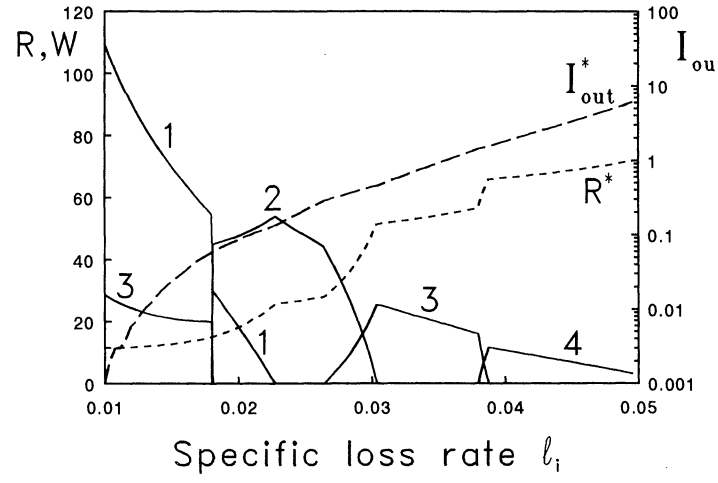

FIG. 8.—The outcome of competition among four species as a function of the specific loss rate. (Compare with fig. 3*E*.) The solid lines indicate the equilibrium biomasses of the species. The two dashed lines indicate the equilibrium nutrient concentration and light penetration. The species are the same as in fig. 5. Environmental parameters: $D = 0.01$; $z = 0.1$; $I_{in} = 10$; $R_{in} = 75$; $K_{bg} = 0$.

light : nutrient conditions on top of a water column to low light : nutrient conditions at the bottom. One might argue that, in spite of the spatial heterogeneity of a light gradient, individual algal cells do in essence face homogeneous conditions, as mixing is much faster than individual growth and reproduction. We do not agree with this position. Algal production is directly related to photosynthesis. It is therefore not the timescale of reproduction that matters, but the timescale on which photosynthesis takes place. Photosynthesis is a very fast process, much faster than the mixing rate. As a consequence, individual algal cells do experience the spatial variability in light intensity, and this spatial heterogeneity must explicitly be taken into account.

Although nutrient consumption and light absorption take place on a local level, not all local interactions have to be known in order to evaluate the conditions for phytoplankton growth. Our key result shows that the growth requirements of a phytoplankton species in a mixed water column can be summarized in terms of the nutrient availability and the light penetration to the bottom of the mixed layer. Each species has its own minimal nutrient and light requirements. These minimal requirements determine not only monoculture growth but also the outcome of competition.

We have framed the minimal light requirements of a species in terms of light penetration to the bottom of the water column (I^*_{out}). In case of mixing, there is a simple relationship between the light intensity at the bottom and the average light intensity, $\bar{I}$, within the column:

$$\bar{I} = \frac{I_{in} - I_{out}}{\ln(I_{in}) - \ln(I_{out})}. \tag{15}$$

Hence, I_{out} and $\bar{I}$ are two equivalent summary variables of the same light gradient. As a consequence, the minimal light requirements of a species can also be characterized in terms of a critical average light intensity ($\bar{I}^*$). Via equation (15), all our results based on I^*_{out} immediately carry over to $\bar{I}^*$. In particular, an isocline based on $\bar{I}^*$ also varies with the incident light intensity, I_{in}.

Framing competition in terms of minimal resource requirements has important conceptual implications. First, our model still predicts that the number of coexisting species cannot exceed the number of limiting resources. Hence, the spatial heterogeneity caused by a light gradient is not sufficient to solve Hutchinson's paradox of the plankton. This conclusion should be quite robust, because we allowed for many possible interactions between nutrient and light limitation. Apparently, incomplete mixing or nonequilibrium conditions must be invoked to explain the species diversity observed in phytoplankton communities.

Second, our model predicts that phytoplankton species become separated along environmental gradients according to their minimal nutrient and light requirements. Because factors such as nutrient supply, mixing depth, and turbidity affect the availability of nutrients and light, these factors should also have a profound impact on phytoplankton community structure.

Mechanisms of Competition for Nutrients and Light

A major advantage of the approach advocated in this article is that the outcome of competition can be predicted without a detailed physiological knowledge of the interactions between nutrient and light limitation. In our model, the outcome of competition is predicted on the basis of the minimal nutrient and light requirements, which can be measured in monoculture experiments. In this respect, our approach is an extension of earlier work on competition for homogeneously distributed nutrients (e.g., Phillips 1973; Tilman 1982; Butler and Wolkowicz 1987). The major difference between our model and this earlier work is related to the spatial heterogeneity imposed by a light gradient. As a consequence of this heterogeneity, the basic ingredients of the graphical isocline approach (isoclines, consumption vectors, supply point) are no longer independent of one another. This makes it difficult to assess graphically how the species composition is affected by changes in environmental parameters. In particular, the resource-ratio hypothesis does not extend to light limitation. Tilman (1982, 1985, 1988) suggested that resource ratios are a simple but fairly robust approximation to predict the outcome of competition. In contrast, our model shows that it is not only the ratio of nutrient supply to light supply that matters but also the absolute supply rates, and that the outcome of competition is also affected by factors such as mixing depth and background turbidity. Furthermore, unexpected changes in the species distribution may be observed along environmental gradients. For example, a species may be a successful competitor when there is a high or a low light supply, but not in between.

While detailed physiological knowledge may not be essential for predicting the outcome of competition, it will certainly provide insights into the physiological constraints and trade-offs underlying the minimal resource requirements. This information might indicate whether some species assemblages are more likely

than others. Consider, for example, the two scenarios illustrated in figures 5 and 6. Both scenarios assume a trade-off between maximal growth rate and shade tolerance. A similar trade-off between maximal growth rate and nutrient affinity is assumed in figure 6 but not in figure 5. This leads to completely different species distributions. If physiological evidence favored one scenario over the other, generalizations about species distribution patterns along resource supply gradients would come into reach.

Physiological knowledge may also help us to investigate the question of whether stable coexistence (fig. 4*A*) is more likely than contingent competitive exclusion (fig. 4*B*). The possibility of stable coexistence depends crucially on the interplay of the consumption, production, and loss characteristics of the competing species. Our model makes no restrictions on the relation between the consumption and growth parameters. In reality, however, consumption is closely linked to growth. Perhaps physiological information on this relationship will provide clues about whether to expect stable coexistence or outcomes depending on the initial conditions.

Empirical Evidence

Numerous studies have shown that environmental factors such as nutrient supply, mixing depth, and turbidity may have a profound impact on the dynamics and structure of phytoplankton communities (reviewed in, e.g., Hutchinson 1967; Kalff and Knoechel 1978; Tilman et al. 1982; Reynolds 1984; Sommer 1989).

For example, Reynolds et al. (1983, 1984) studied the response of phytoplankton to alternating phases of mixing and restratification. Diatoms, desmids, and *Oscillatoria* achieved rapid growth rates during mixing but declined during quiescent, restratifying episodes. In contrast, the green algae *Eudorina* and *Sphaerocystis* grew well during quiescent periods but declined during the mixing episodes. Reynolds and colleagues concluded that the impact of mixing operated through its relationship with light availability.

Cuker (1987) studied the effects of clay and phosphorus loading on the algal community of a small freshwater lake. Clay loading reduced net primary production and algal cell densities. Suspended clay also caused a shift in community composition; flagellates replaced the otherwise dominant *Spirulina major*. In contrast, phosphorus loading increased algal densities and favored development of nitrogen-fixing *Anabaena* species.

Sommer (1988) related the distribution of 12 antarctic phytoplankton species to resource ratios and mixing depth. Eight of these species showed a significant correlation with one or more nutrient ratios, five species were significantly correlated with mixing depth, and only one species was correlated with a nutrient : light ratio.

Reynolds (1987) fitted the occurrence of various groups of phytoplankton species to the ambient nutrient and light availability. His figures show a remarkable resemblance to our figures 5*C* and 6*C*. For example, the distribution of species 4 in figure 5*C* is reminiscent of the distribution of many chrysophytes (*Dinobryon, Uroglena*) and colonial chlorophytes (*Sphaerocystis, Gemellicystis*), while our species 1 resembles an *Oscillatoria* species. However, a full evaluation of these distribution patterns in the context of our model is not yet possible. For this

purpose, information on the nutrient affinities and photosynthetic rates of the species concerned (as in figs. 5*A*, *B* and 6*A*, *B*) would be required.

The examples given above seem qualitatively consistent with our model predictions. This is encouraging. On the other hand, it is clear that our model is an extreme simplification of the complexity encountered in any natural system. For instance, our model does not consider the daily and seasonal fluctuations of the light supply (van Gemerden 1974; Brzezinski and Nelson 1988), the spectral distribution of light (Montesinos et al. 1983), incomplete mixing and algal motility (Reynolds 1984; Weissing and Huisman 1994), feedback between algal biomass and mixing depth (Mazumder et al. 1990), mutual flocculation of algae and clay (Avnimelech et al. 1982; Cuker et al. 1990), variable tissue nutrient concentrations (Droop 1973; Grover 1991), heterotrophic nutrition by flagellate species (Sanders and Porter 1988), density-dependent losses due to grazers and pathogens (Sterner 1989; Suttle et al. 1990), or resource-dependent sinking rates (Titman and Kilham 1976). In principle, these additional components could be incorporated into the model framework.

Here we have left out these additional complexities in order to focus on the fundamental interactions between nutrient and light limitation. We are confident that the qualitative insights will prove useful for understanding the dynamics and structure of phytoplankton communities. In view of the restrictions mentioned above, the model may be less appropriate for quantitative predictions in natural field situations. But even the quantitative predictions could be tested in controlled laboratory experiments in which phytoplankton is grown under constant, well-mixed conditions. The experimental procedure is straightforward. First, monocultures should be grown at various nutrient supply rates until they reach a steady state. Light penetration and nutrient concentration in the steady state provide the data to draw the isoclines. Together with measurements of light absorption and nutrient consumption, this allows a priori predictions of the outcome of competition. In the next step, these predictions could be put to a test simply by performing the competition experiments. As far as we know, nobody has ever performed competition experiments in which phytoplankton species competed for both nutrients and light. We are not even aware of monoculture experiments that provide sufficient information to derive the isocline of a species. We hope that our analysis provides a challenge for further experimentation.

ACKNOWLEDGMENTS

We are grateful to J. van Andel, L. Mur, C. Reynolds, R. Sterner, and D. Tilman for their helpful comments. The research of J.H. was supported by the Life Sciences Foundation (SLW), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

APPENDIX A

Shape of the Isoclines

BIOMASS ISOCLINE

The slope of the biomass isocline in the (R, W) plane can be obtained by differentiating both sides of the isocline equation $dW/dt = 0$ with respect to R. This yields

$$\frac{\partial P}{\partial R} + \frac{\partial P}{\partial W}\frac{dW}{dR} - \ell\frac{dW}{dR} = 0.$$

In view of equation (3), the slope of the biomass isocline is thus given by

$$\frac{dW}{dR} = -\frac{\partial P/\partial R}{g(I_{\text{out}}, R)}.$$

The numerator is positive, since

$$\frac{\partial P}{\partial R} = \int_0^W \frac{\partial p}{\partial R}(I(w), R)\,dw > 0.$$

In view of equation (8), the denominator is negative. Hence, the biomass isocline has a positive slope.

NUTRIENT ISOCLINE

Implicit differentiation of $dR/dt = 0$ with respect to W yields

$$-D\frac{dR}{dW} - \frac{c}{z}\left(\frac{\partial P}{\partial R}\frac{dR}{dW} + \frac{\partial P}{\partial W}\right) = 0.$$

The slope of the nutrient isocline is thus given by

$$\frac{dR}{dW} = -\frac{cp(I_{\text{out}}, R)}{Dz + c(\partial P/\partial R)}.$$

Both numerator and denominator are positive. Hence, the slope of the nutrient isocline is negative.

ISOCLINE IN (R, I_{out}) PLANE

Implicit differentiation of $Q(I_{\text{out}}, R) = 0$ with respect to R gives the slope of the biomass isocline in the (R, I_{out}) plane:

$$\frac{dI_{\text{out}}}{dR} = -\frac{\partial Q/\partial R}{\partial Q/\partial I_{\text{out}}}. \tag{A1}$$

In view of equations (7) and (6),

$$\frac{\partial Q}{\partial R} = \int_{I_{\text{out}}}^{I_{\text{in}}} \frac{1}{kI}\frac{\partial p}{\partial R}(I, R)\,dI > 0.$$

Application of the fundamental theorem of calculus shows that

$$\frac{\partial Q}{\partial I_{\text{out}}} = -q(I_{\text{out}}, R) > 0.$$

Thus, the biomass isocline in the (R, I_{out}) plane has a negative slope.

APPENDIX B

Patterns along a Nutrient Supply Gradient

This appendix illustrates how the qualitative patterns depicted in figure 3 can be obtained analytically. The equilibrium biomass, light penetration, and nutrient concentration are implicit functions of the model parameters. For example, implicit differentiation of the equilibrium equations

$$\frac{dR}{dt} = D(R_{\text{in}} - R^*) - \frac{c}{z}P(R^*, W^*) = 0$$

and

$$\frac{dW}{dt} = P(R^*, W^*) - \ell W^* = 0$$

with respect to R_{in} yields

$$D - D\frac{dR^*}{dR_{\text{in}}} - \frac{c}{z}\left(\frac{\partial P}{\partial R}\frac{dR^*}{dR_{\text{in}}} + \frac{\partial P}{\partial W}\frac{dW^*}{dR_{\text{in}}}\right) = 0$$

and

$$\frac{\partial P}{\partial R}\frac{dR^*}{dR_{\text{in}}} + \frac{\partial P}{\partial W}\frac{dW^*}{dR_{\text{in}}} - \ell\frac{dW^*}{dR_{\text{in}}} = 0.$$

These two equations can be solved:

$$\frac{dW^*}{dR_{\text{in}}} = \frac{\partial P/\partial R}{\frac{c\ell}{zD}\frac{\partial P}{\partial R} - g(I^*_{\text{out}}, R^*)}$$

and

$$\frac{dR^*}{dR_{\text{in}}} = \frac{-g(I^*_{\text{out}}, R^*)}{\frac{c\ell}{zD}\frac{\partial P}{\partial R} - g(I^*_{\text{out}}, R^*)}.$$

The numerators and denominators are positive, since $\partial P/\partial R > 0$ and $g(I^*_{\text{out}}, R^*) < 0$. This shows that $dW^*/dR_{\text{in}} > 0$ and $dR^*/dR_{\text{in}} > 0$. In other words, the biomass and the nutrient availability in the steady state are both positively related to the nutrient supply, as illustrated in figure 3*A*. Furthermore, according to Lambert-Beer's law,

$$\frac{dI^*_{\text{out}}}{dR_{\text{in}}} = -kI^*_{\text{out}}\frac{dW^*}{dR_{\text{in}}}.$$

Hence, the steady-state light penetration is negatively related to the nutrient supply.

Via a similar approach, the other trends depicted in figure 3 can also be derived analytically (J. Huisman, unpublished results).

APPENDIX C

Stability of the Monoculture Equilibrium

In order to establish the local stability of the interior monoculture equilibrium, we investigate the Jacobian matrix of the system. If we write dW/dt and dR/dt as $\dot{W}$ and $\dot{R}$, respectively, the elements of the Jacobian matrix are given by

$$A_{11} = \left(\frac{\partial \dot{W}}{\partial W}\right)^* = g(I^*_{\text{out}}, R^*) < 0,$$

$$A_{12} = \left(\frac{\partial \dot{W}}{\partial R}\right)^* = \int_0^{W^*} \frac{\partial p}{\partial R}(I(w), R^*)\, dw > 0,$$

$$A_{21} = \left(\frac{\partial \dot{R}}{\partial W}\right)^* = -\frac{c}{z} p(I^*_{\text{out}}, R^*) < 0,$$

and

$$A_{22} = \left(\frac{\partial \dot{R}}{\partial R}\right)^* = -D - \frac{c}{z}\int_0^{W^*} \frac{\partial p}{\partial R}(I(w), R^*)\, dw < 0.$$

The superscript asterisk indicates that the matrix is evaluated at equilibrium. According to the Routh-Hurwitz criteria (see, e.g., Edelstein-Keshet 1988), local stability requires that $A_{11} + A_{22} < 0$ and $A_{11}A_{22} - A_{12}A_{21} > 0$. In view of the sign pattern of the matrix elements, this is indeed the case. Hence, the interior equilibrium is stable whenever it exists.

APPENDIX D

Stability of the Coexistence Equilibrium

In this appendix, we investigate the local stability of the coexistence equilibrium. In order to write the elements of the Jacobian matrix in a convenient form, we use the following information: the coexistence equilibrium is characterized by $Q_i(I^*_{\text{out}}, R^*) = 0$; according to Lambert-Beer's law, $\partial I_{\text{out}}/\partial W_1 = (k_1/k_2)(\partial I_{\text{out}}/\partial W_2)$; we introduce $\alpha_i = k_i W_i^*/(\Sigma k_j W_j^* + K_{\text{bg}} z)$; for P_i^* we substitute $\alpha_i Q_i(I^*_{\text{out}}, R^*) + \ell_i W_i^*$. Hence, the elements of the Jacobian matrix are given by

$$A_{11} = \left(\frac{\partial \dot{W}_1}{\partial W_1}\right)^* = \alpha_1 \frac{\partial Q_1}{\partial I_{\text{out}}}\frac{\partial I_{\text{out}}}{\partial W_1} < 0,$$

$$A_{12} = \left(\frac{\partial \dot{W}_1}{\partial W_2}\right)^* = \frac{k_2}{k_1} A_{11} < 0,$$

$$A_{13} = \left(\frac{\partial \dot{W}_1}{\partial R}\right)^* = \alpha_1 \frac{\partial Q_1}{\partial R} > 0,$$

$$A_{21} = \left(\frac{\partial \dot{W}_2}{\partial W_1}\right)^* = \frac{k_1}{k_2} A_{22} < 0,$$

$$A_{22} = \left(\frac{\partial \dot{W}_2}{\partial W_2}\right)^* = \alpha_2 \frac{\partial Q_2}{\partial I_{\text{out}}}\frac{\partial I_{\text{out}}}{\partial W_2} < 0,$$

$$A_{23} = \left(\frac{\partial \dot{W}_2}{\partial R}\right)^* = \alpha_2 \frac{\partial Q_2}{\partial R} > 0,$$

$$A_{31} = \left(\frac{\partial \dot{R}}{\partial W_1}\right)^* = -\frac{c_1}{z}(A_{11} + \ell_1) - \frac{c_2}{z}A_{21},$$

$$A_{32} = \left(\frac{\partial \dot{R}}{\partial W_2}\right)^* = -\frac{c_1}{z}A_{12} - \frac{c_2}{z}(A_{22} + \ell_2),$$

$$A_{33} = \left(\frac{\partial \dot{R}}{\partial R}\right)^* = -D - \frac{c_1}{z}A_{13} - \frac{c_2}{z}A_{23} < 0.$$

According to the Routh-Hurwitz criteria (see, e.g., Edelstein-Keshet 1988), stability requires (1) $a_1 > 0$, (2) $a_3 > 0$, and (3) $a_1a_2 - a_3 > 0$, where

$$a_1 = -A_{11} - A_{22} - A_{33},$$

$$a_2 = A_{11}A_{22} + A_{11}A_{33} + A_{22}A_{33} - A_{12}A_{21} - A_{23}A_{32} - A_{13}A_{31},$$

and

$$a_3 = -A_{11}A_{22}A_{33} + A_{11}A_{23}A_{32} + A_{22}A_{31}A_{13} + A_{33}A_{12}A_{21} - A_{12}A_{31}A_{23} - A_{13}A_{21}A_{32}.$$

Criterion 1.—In view of the sign pattern of the matrix elements, it is obvious that $a_1 > 0$.

Criterion 2.—In our case, a_3 is given by

$$a_3 = (k_1A_{22}A_{13} - k_2A_{11}A_{23})\left(\frac{1}{k_1}A_{31} - \frac{1}{k_2}A_{32}\right)$$

$$= \frac{I^*_{\text{out}}}{z}k_1\alpha_1k_2\alpha_2\left(\frac{\partial Q_1}{\partial I_{\text{out}}}\frac{\partial Q_2}{\partial R} - \frac{\partial Q_2}{\partial I_{\text{out}}}\frac{\partial Q_1}{\partial R}\right)\left(\frac{c_2\ell_2}{k_2} - \frac{c_1\ell_1}{k_1}\right).$$

Remember that we labeled the species in such a way that, at the point of intersection, the slope of the isocline of species 2 is steeper than the slope of the isocline of species 1. In view of equation (A1), this means

$$\frac{\partial Q_2/\partial R}{\partial Q_2/\partial I_{\text{out}}} > \frac{\partial Q_1/\partial R}{\partial Q_1/\partial I_{\text{out}}}. \tag{D1}$$

Hence, criterion 2 is satisfied if and only if

$$\frac{c_2\ell_2}{k_2} > \frac{c_1\ell_1}{k_1}.$$

If this inequality is reversed, the coexistence equilibrium is unstable.

Criterion 3.—The coefficient a_2 can be written as

$$a_2 = \frac{1}{z}(k_1A_{22}A_{13} - k_2A_{11}A_{23})\left(\frac{c_2}{k_2} - \frac{c_1}{k_1}\right) - D(A_{11} + A_{22}) + \frac{c_1}{z}\ell_1A_{13} + \frac{c_2}{z}\ell_2A_{23}.$$

Hence,

$$a_1a_2 - a_3 = a_1\frac{1}{z}(k_1A_{22}A_{13} - k_2A_{11}A_{23})\left(\frac{c_2}{k_2} - \frac{c_1}{k_1}\right) - a_1D(A_{11} + A_{22}) - \frac{c_1}{z}\ell_1A_{13}(A_{11} + A_{33})$$

$$- \frac{c_2}{z}\ell_2A_{23}(A_{22} + A_{33}) - \frac{c_1}{z}\frac{k_2}{k_1}\ell_1A_{11}A_{23} - \frac{c_2}{z}\frac{k_1}{k_2}\ell_2A_{22}A_{13}.$$

All terms, except the first, are positive. Criterion 3 is thus certainly satisfied if the first term is also positive. In view of inequality (D1), this will be the case if $c_1/k_1 < c_2/k_2$.

Now suppose that $c_1/k_1 > c_2/k_2$. After some algebra, the above equation can be rewritten as $a_1a_2 - a_3 = \beta + \gamma + \delta + \epsilon$, where

$$\beta = -a_1D(A_{11} + A_{22}) - \frac{c_1}{z}\ell_1A_{13}(A_{11} + A_{33}) - a_1\frac{c_2}{z}A_{11}A_{23} + \frac{c_1}{z}A_{13}A_{22}^2,$$

$$\gamma = \frac{1}{z}k_1A_{22}A_{13}\left(\frac{c_1}{k_1} - \frac{c_2}{k_2}\right)(A_{11} + A_{33}),$$

$$\delta = -\frac{c_1}{z}\frac{k_2}{k_1}A_{23}A_{11}(A_{11} + \ell_1) - \frac{c_2}{z}\frac{k_1}{k_2}A_{13}A_{22}(A_{22} + \ell_2),$$

and

$$\epsilon = -\frac{k_2}{z}A_{23}\left(\frac{c_1}{k_1}A_{11} + \frac{c_2}{k_2}\ell_2\right)(A_{22} + A_{33}).$$

From the sign pattern of the matrix elements it is obvious that $\beta > 0$. Since we consider $c_1/k_1 > c_2/k_2$, we also have $\gamma > 0$. Since $A_{11} = \alpha_1 g_1(I^*_{out}, R^*)$, with $0 < \alpha_1 < 1$, and $g_1(I^*_{out}, R^*) + \ell_1 > 0$, we have $A_{11} + \ell_1 > 0$. Similarly, $A_{22} + \ell_2 > 0$. Hence, $\delta > 0$. Finally, if we may assume $c_2\ell_2/k_2 > c_1\ell_1/k_1$, then also $\epsilon > 0$. Thus, criterion 3 is certainly satisfied for $c_1/k_1 < c_2/k_2$, and it is also satisfied for $c_1/k_1 > c_2/k_2$ if $c_2\ell_2/k_2 > c_1\ell_1/k_1$.

Conclusion.—Coexistence is locally stable if $c_2\ell_2/k_2 > c_1\ell_1/k_1$ and locally unstable if this inequality is reversed.

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